Changes in organic chemical components of needle litter during decomposition. Long-term decomposition in a Scots pine forest. I

BJÖRN BERG[1]
Swedish Coniferous Forest Project and Department of Microbiology, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden
KAI HANNUS[2]
The Institute of Wood Chemistry and Cellulose Technology, Åbo Akademi, Åbo, Finland
AND
THOMAS POPOFF[3] AND OLOF THEANDER
Department of Chemistry and Molecular Biology, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

Received April 23, 1981

BERG, B., K. HANNUS, T. POPOFF, and O. THEANDER. 1982. Changes in organic chemical components of needle litter during decomposition: long-term decomposition in a Scots pine forest I. Can. J. Bot. **60**: 1310–1319.

The decomposition and organic chemical changes in Scots pine (*Pinus silvestris*) needle litter were studied for a period of 5 years and until 75% weight loss was reached in field incubation. The changes in components such as various groups of lipophilic extractives, low-molecular carbohydrates, cyclitols, phenolic glycosides, polysaccarides, and lignin were followed. There was a great drop of sugars, steryl esters, and triglycerides during the 1st year of decomposition. Some isoprenoid alcohols, sterols, and some acids belonged to the most stable of the soluble components. Of the solid residue the arabinans decomposed rapidly, the cellulose decomposed somewhat faster than the hemicelluloses as a group, and the lignin decomposed rather slowly (about 48% in 5 years).

BERG, B., K. HANNUS, T. POPOFF et O. THEANDER. 1982. Changes in organic chemical components of needle litter during decomposition: long-term decomposition in a Scots pine forest I. Can. J. Bot. **60**: 1310–1319.

La décomposition de la litière d'aiguilles de pin sylvestre (*Pinus silvestris*) et les changements chimiques dans les composés organiques de la litière ont été étudiés pendant une période de 5 ans, et jusqu'à une perte en poids de 75% dans les incubations au champ. Les changements de divers types de composés chimiques ont été suivis: extraits lipophiles, glucides de faible poids moléculaire, cyclitols, glycosides phénoliques, polysaccarides et lignine. Il y a une forte baisse des sucres, des stéryl esters et des triglycérides au cours de la première année de décomposition. Certains alcools isoprénoïdes, des stérols et quelques acides sont parmi les plus stables des composés solubles. Quant aux résidus solides, les arabinanes se décomposent rapidement, la cellulose se décompose un peu plus vite que l'hémicellulose, tandis que la lignine se décompose plutôt lentement (environ 48% en 5 ans).

[Traduit par le journal]

Introduction

Litter and humus are organic chemical carriers of nutrients and their decomposition appears to be the limiting process for the release of nutrients. However, comparatively little is known about the decomposition of plant litter in nature. The chemical composition, both the inorganic and the organic, could be expected to be an important regulatory factor for the rate of the decomposition process and some of the studies made have dealt with decomposition versus the organic and inorganic composition of the litter. However, in spite of numerous studies and comments on the effect of "chemical–physical" quality of litter on decomposition there have been very few studies on the decomposition of specific chemical components of litter. Melin (1928) found that the percentage of nitrogen in litters strongly affected the weight loss rate. He also suggested that decomposition is affected by other factors, among which tannins have been assumed to affect weight loss rate in oak leaves (Harrison 1971). High levels of lignin have a strong negative influence on decomposition rate, and Fogel and Cromack (1977) found it to be more rate determining than the C/N quotient or total nitrogen content. In Scots pine needle litter, Berg and Staaf (1980) found that the nutrient level stimulated weight loss only initially whereas in later stages the lignin level had a retarding effect that probably overtook the effect of nutrient level as decomposition proceeded. It was also suggested (Berg and Staaf 1981) that the magnitude of nutrient immobilization and release was strongly dependent on

---

[1] Present address: Section of Forest Ecology, Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden.

[2] Present address: Raision Tehtaat OY, SF-21 200 Raisio, Finland.

[3] Present address: Waters Associates AB, Sommarvägen 5, S-171 40 Solna, Sweden.

0008-4026/82/081310-10$01.00/0

©1982 National Research Council of Canada/Conseil national de recherches du Canada

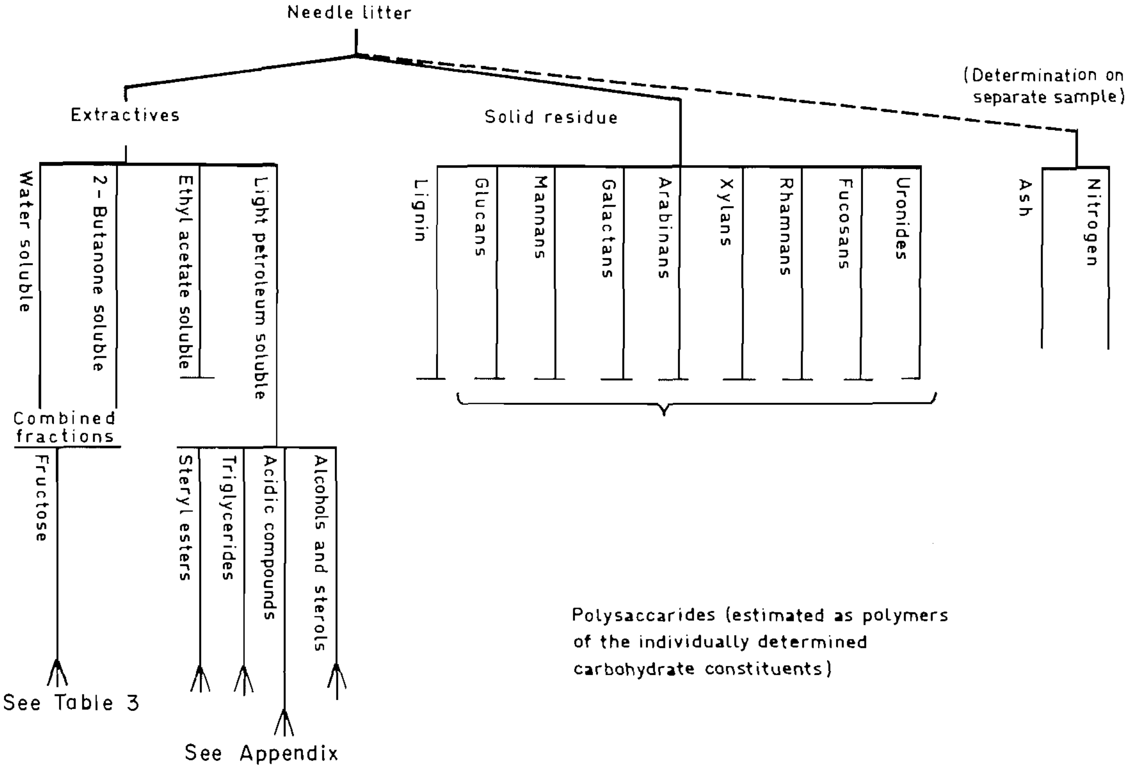

FIG. 1. An overview of the organic chemical analyses.

decomposition rate and thus on the organic chemical composition.

The decomposition of major chemical components has been studied to some extent. Tenney and Waksman (1929) incubated mainly agricultural litters under optimized laboratory conditions and measured the decomposition of soluble material, hemicelluloses, cellulose, and lignin. Swanger (1974) investigated the same components of decomposing hemlock litter after 220 days under laboratory conditions. The polyphenol content of decomposing pine needle litter has been studied by Hayes (1965) who found it to decrease during the 1st year, with a heavy initial drop. The levels of the polyphenolic substances in needles have been suggested to vary with the nutrient status of the soil (Staaf and Berg 1981; Gosz 1981): high polyphenol levels on poor soils and low polyphenol levels on rich ones.

The litter bag as a means to measure litter decomposition was discussed thoroughly by Louisier and Parkinson (1976) and different method studies about the litter-bag technique were discussed. At present it appears reasonable to conclude that a large factor for errors is the net's mesh size versus the soil animals' influence on decomposition at a certain site. In the case of a soil fauna taking an active part in litter degradation, the mesh size of the litter bag should admit passage of the animals unless their exclusion is specifically required.

In the present study the forest stand has a soil fauna of which few species could affect the decomposition rate in the litter bags. The mites have been shown to cause a decrease in weight loss rate, although the effect was small (Berg, Lohm *et al.* 1980). They can, on the other hand, move freely through the litter-bag net. The nutrient-poor Scots pine (*Pinus silvestris*) stand was described in detail by Axelsson and Bråkenhielm (1980).

The aim of the present investigation, connected with the Swedish Coniferous Forest Project (Anonymous 1974), was to follow the organic chemical composition of needle litter of Scots pine during decomposition on the forest floor. A preliminary report on part of this work already has been published (Theander 1978). We have also recently reported a thorough characterization of green and brown needles from the trees of the present site as well as studies on the microbial response to soluble fractions from these needles (Berg, Hannus *et al.* 1980).

Materials and methods

Site description

The 120- to 130-year-old Scots pine stand studied is located at the Swedish Coniferous Forest Project research site, Ivantjärnsheden, central Sweden (60°49′ N, 16°30′ E) at an altitude of 185 m on a flat area of deep glacifluvial sand

TABLE 1. Weight loss and changes in some major analytical

	Date of sampling					
	74 05 12	74 09 02	74 11 03	75 05 13	75 10 29	76 04 28
Days of incubation	0	123	185	376	545	726
Weight loss[a]	0	10.4	17.8	27.3	43.2	44.4
SE	—	0.23	0.89	1.16	1.05	0.83
Solid residue						
Relative[b]	73.2	74.4	79.6	83.0	87.6	87.1
Absolute[d]	732	667	654	603	498	484
Extractives						
Relative	27.2	28.6	28.8	22.2	15.0	17.1
Absolute	272	256	237	161	85	95
Nitrogen						
Relative	0.38	0.37	0.48	0.62	0.85	0.79
Absolute	3.8	3.32	3.95	4.51	4.83	4.39
Ash						
Relative	2.3	2.2	2.2	2.5	2.4	2.1
Absolute	23	20	18	18	14	12

[a] As percent of original weight.

[b] As percent of the sample.

[c] Not determined.

[d] Milligrams as remaining of 1000 mg initial litter.

sediments. The mean annual precipitation at a nearby village is 609 mm (1931–1960) and the mean annual temperature is +3.8°C. The length of the growing season is about 160 days (number of days with a daily temperature higher than 6°C; Axelsson and Bråkenhielm 1980).

The tree layer is exclusively composed of *Pinus silvestris* L. and has a density of 393 trees per ha and a height of 17–19 m. *Calluna vulgaris* and *Vaccinium vitis-idaea* form a well-developed field layer, and the bottom layer, completely covering the ground, is mainly composed of the mosses *Pleurozium schreberi* and *Dicranum rugosum* together with *Cladonia* lichens. The most recent direct effect of forestry practices was a slight thinning in 1960. A more complete description is given by Axelsson and Bråkenhielm (1980).

The soil profile is an orthic humoferric podzol (iron podzol) with a weakly developed A_e horizon (bleached horizon; 2–7 cm) and the humus form is a typical mor. A very loose L horizon (A_{00}), interwoven with living mosses and lichens, covers an F/H horizon (A_{01}–A_{02}) of 5–10 cm. The F horizon (A_{01}) and the H horizon (A_{02}) are almost indistinguishable from each other. The pH range is 3.9–4.2 in the F/H horizon and 4.6–4.8 in the upper mineral soil. The parent mineral material as well as the whole soil is considered to be very poor in essential nutrients. The C/N ratio of the F/H horizon (A_{01}–A_{02}) is 42.3.

Needle collection, storage, and sample preparation

Brown needles were sampled at Ivantjärnsheden in late October 1973 from the branches of about 15-year-old Scots pines at abscission, air dried, and stored at −20°C until the sample preparation took place. The trees were all located in an area less than 20 × 50 m^2.

Before weighing, the needles were dried at room temperature to reach an even moisture level (6.94%). The biggest difference in moisture was less than ±0.5% from the average as determined on 20 samples.

The litter bags measuring 8 × 8 cm were made of terylene net with a mesh size of 1 mm. Each litter bag enclosed an amount of about 2 g of needle litter and a piece of plastic tape giving the weight of the needles. The bags were fastened to the ground by 10- to 15-cm-long metal pins and were incubated for 123, 185, 376, 545, 726, 845, 922, 1125, 1228, 1273, 1480, 1581, 1627, and 1825 days.

Sampling and chemical analysis

The samples were placed on the A_{00} layer at 20 test spots (1 × 1 m^2) randomly selected among 300 in the 120-year-old stand in spring as soon as the snow had melted (May 12, 1974).

For weight loss determinations one sample from each of the 20 test spots were collected, transported directly to the laboratory, and cleaned of mosses, lichens, and lingonberry remnants. At some of the samplings half a needle was taken out per sample for determination of invading mycelium (Berg and Söderström 1979). After the removal of plant remains, the loss of dry weight of the needles was determined by drying the aliquots to constant weight at 85°C. The nitrogen determinations were done by Kjeldahl analysis and the ash contents by heating at 600°C for 3 h.

Organic chemical analyses were performed on separate sets of litter, collected as above, but air-dried. The amount of needles was 200 g (10 litter bags from each spot; samples of needles decomposed for 0–376 days) and 20–40 g (2 litter bags from each spot; samples decomposed for more than 376 days). In a typical procedure for the 200-g sets (Fig. 1), fractions of Scots pine needle litter during decomposition

76 08 25	76 11 10	77 06 01	77 09 12	77 10 27	78 05 22	78 08 31	78 10 16	79 05 14
845	922	1125	1228	1273	1480	1581	1627	1825
51.2	55.8	58.8	63.0	63.8	66.5	70.8	71.4	75.0
1.24	1.19	1.65	1.30	0.88	1.27	1.61	1.55	0.94
85.0	89.3	nd[c]	85.9	84.1	84.7	85.3	85.9	83.5
415	395	—	318	304	284	249	246	209
16.0	13.2	nd	16.0	16.1	15.4	14.7	14.1	16.3
78	58	—	59	58	52	43	40	41
0.92	0.99	0.96	1.02	1.18	1.12	1.16	1.21	1.25
4.49	4.38	3.96	3.77	4.27	3.75	3.39	3.46	3.13
2.4	2.7	nd	2.8	2.7	3.4	3.4	3.3	3.3
12	12	—	10	10	11	10	10	9

needles were milled and extracted first with acetone (three times 700 mL for 30 min) and then with 50% aqueous acetone (three times 700 mL for 30 min) in an ultrasonic bath at room temperature. The combined extracts were evaporated to a small volume (aqueous solution–suspension) and by extractions divided into fractions comprising compounds soluble in light petroleum (bp 40–60°C), ethyl acetate, 2-butanone (saturated with water), and those left in the water (Popoff and Theander 1977). All evaporations were done at reduced pressure (below 40°C). The sets of 20–40 g were extracted as above.

After extraction the dried residues were analysed for sulphuric acid lignin (Klason lignin) and carbohydrates by hydrolysis (12.0 *M* H_2SO_4 at room temperature for 2 h and refluxed for 6 h after dilution to 0.358 *M*), and a quantitative determination of the neutral sugars in the hydrolysate was performed after reduction and acetylation by gas–liquid chromatography (Bethge *et al.* 1971). The polyuronide contents were determined by a decarboxylation method (Bylund and Donetzhuber 1968).

The light petroleum extractives were separated into neutral and acidic compounds and further into major groups (hydrocarbons, steryl esters, triglycerides, fatty and diterpene acids, sterols, and diterpene alcohols) as described previously (Hannus and Pensar 1974).

The contents of phenolic glycosides in the ethyl acetate, 2-butanone, and water extracts were determined gravimetrically after fractionation on Sephadex LH-20 followed by silicic acid columns. Individual phenolic compounds present were identified by thin-layer chromatography (TLC) as described previously (Popoff and Theander 1977). Low-molecular carbohydrates in the two types of extracts were determined by gas–liquid chromatography after silylation (Theander and Åman 1976).

Leaching experiments

Release of water soluble substances from whole needles was investigated by allowing the needles to soak in distilled water at room temperature for 10 and 24 h. After soaking, dry weight was determined at 85°C.

Results and discussion

Initial organic chemical composition

The organic chemical analysis of the needle litter at this site (Fig. 2) revealed sulphuric acid lignin (Klason lignin) and glucans as dominating components. Of the polymeric non cellulose carbohydrates, mannans, arabinans, and the group of acidic constituents (uronic acids) were the biggest components whereas galactans, xylans, rhamnans, and especially fucosans appeared in small amounts. The determination of the nonglucan constituents was based on analysis of their hydrolysates and for the sake of simplicity they are here presented as individual homoglycans. In the plant material, however, they are probably present mainly as a series of heteroglycans made up of two or more sugars and (or) minor acid units. To some extent also glucose may be present in these noncellulose polysaccharides (mainly so-called hemicelluloses).

The group of extractives was primarily divided into those components either soluble in water, 2-butanone, ethyl acetate, or light petroleum ether. The latter

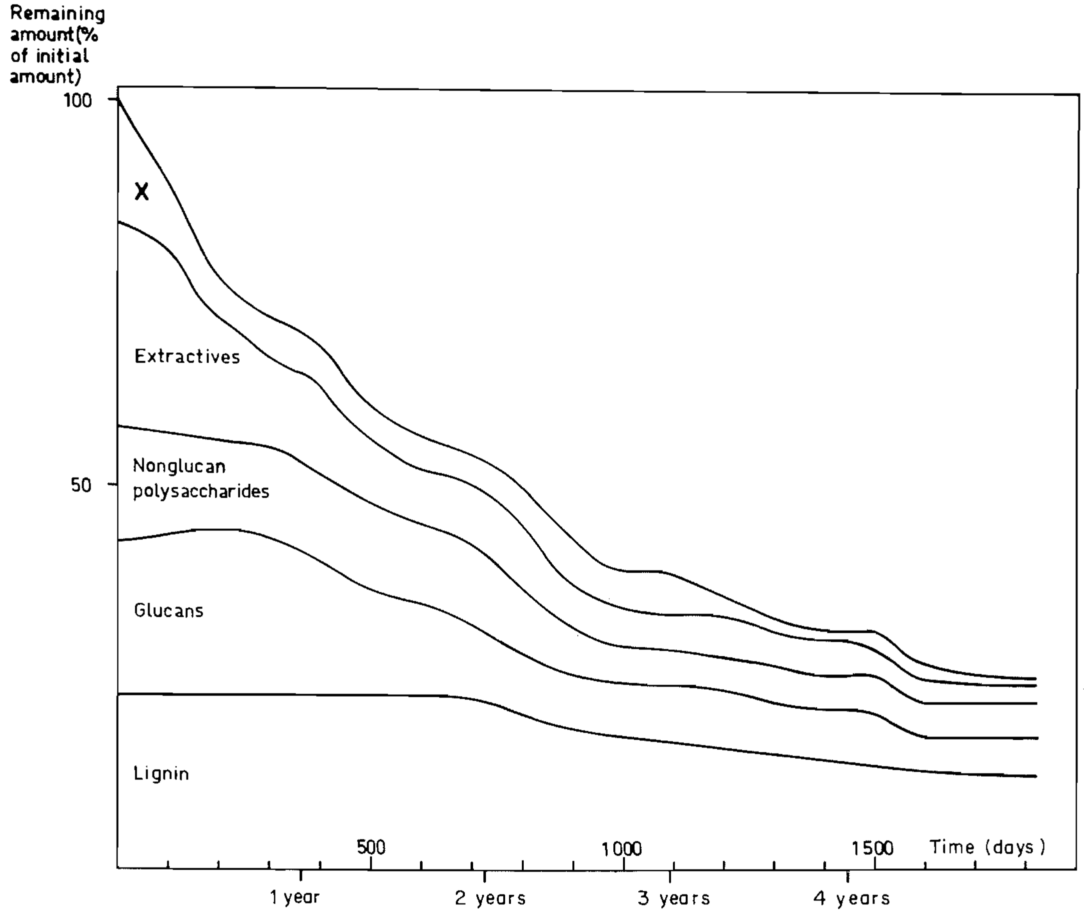

FIG. 2. Survey of changes in composition of Scots pine needle litter during decomposition. × corresponds to crude protein, polyuronides, ash, and unspecified products.

fraction was further divided into subfractions of which the group of acidic compounds appeared to be the largest (Appendix). The microbial response to the contents of these fractions at inhibition tests differed considerably (Berg, Hannus *et al.* 1980). The water soluble and 2-butanone fractions contained components which stimulated the microbial growth in contrast to those of the ethyl acetate fraction which instead decreased the growth rate of fungal hyphae. In the latter case polyphenolic components probably were responsible.

It appears that the literature information about organic chemical composition of forest litters such as leaf and needle litters is limited and, as pointed out by Handley (1954), it sometimes can be difficult to compare studies owing to very different methods of analysis and ways of calculating the analytical results.

The kinetics of weight loss

The weight loss rate of whole litter was rather low with 27% after 1 year and 75% after 5 years (Table 1). In this case no leaching of the litter took place (<1%) and the weight losses were thus due to breakdown of all

TABLE 2. Changes in main groups of extractives during decomposition

	Sample			
	A	B	C	D
Weight loss of litter (%)	0	10.4	17.8	27.3
Light petroleum soluble				
Relative[a]	30.9	22.3	19.8	22.1
Absolute[b]	84.0	57.1	47.0	35.6
Ethyl acetate soluble				
Relative	23.9	33.9	34.0	42.3
Absolute	65.0	86.8	80.6	68.1
2-Butanone soluble				
Relative	11.4	3.1	2.8	—
Absolute	31.0	7.9	6.6	—
Water soluble				
Relative	33.8	40.6	43.4	35.6
Absolute	91.9	103.9	102.9	57.3

[a] Given as percent of dry matter of extractives.
[b] Milligrams as remaining from 1000 mg initial litter.

components kept within the needles' structure. The best regression model for the weight loss so far seen was an exponential function ($1 - e^{-x}$) for the whole 5-year period (B. Berg, in preparation).

Chemical changes during decomposition

Extractives

As the decomposition proceeded marked chemical changes took place in both the fraction of combined extractives and the fraction of remaining solid residue (Table 1, Fig. 2). It is seen from the former that both the amount and percentage of combined extractives decreased with the level of decomposition. Of the extractives, 60% of the initial amount remained after 1 year and only about 15% after 5 years.

The fraction of 2-butanone solubles decreased rather quickly (Table 2), whereas the amount of water soluble substances remained at and above the initial value during the period from May until November. It is possible that freezing and thawing during the winter with a disruption of the needles' cell walls could have made the main part of water solubles more available to the invading microorganisms, the amount of which increase during this period (Berg and Söderström 1979). We cannot, of course, exclude a formation of water soluble substances from decomposing polymers. There might also be an addition to this fraction by the cell contents of microorganisms which became lysed by the ultrasound treatment. Considering the small mycelial amounts of less than 5 mg/g including dead mycelium, we probably can neglect this latter contribution.

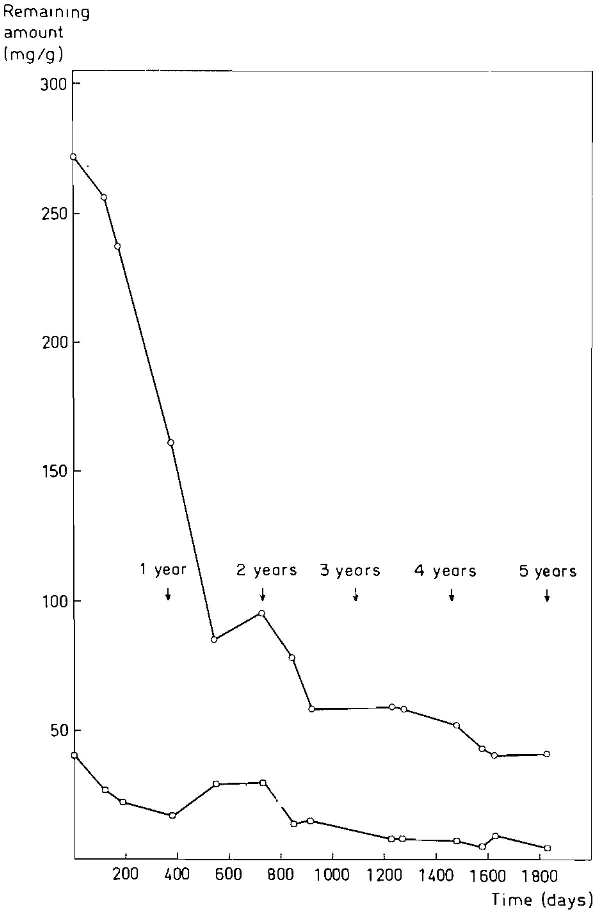

FIG. 3. The degradation of two initially quickly decomposed analysis fractions given as remaining amount from initially 1 g of litter. ○, extractives; □, arabinans.

TABLE 3. Composition of low-molecular carbohydrates and phenol glycosides in the water and 2-butanone fractions

	Sample			
	A	B	C	D
Weight loss of litter (%)	0	10.4	17.8	27.3
Pinitol				
Relative[a]	3.3	0.8	0.8	0.3
Absolute[b]	4.1	0.9	0.9	0.2
Myoinositol				
Relative	0.5	0.2	[c]	[c]
Absolute	0.6	0.2	—	—
Mannitol				
Relative	0.8	1.6	0.8	1.2
Absolute	1.0	1.8	0.9	0.7
Glucose				
Relative	3.3	2.4	1.6	1.1
Absolute	4.1	3.0	2.0	1.4
Fructose				
Relative	4.1	0.1	0	0
Absolute	5.0	0.1	0	0
Sucrose				
Relative	1.6	0.2	0	0
Absolute	2.0	0.2	0	0
Dilignol glycoside				
Relative	1.1	0.1	[c]	0
Absolute	1.4	0.1	—	—
Dihydroquercetin-3′-β-glycoside				
Relative	0.4	[c]	0	0
Absolute	0.5	—	0	0

[a] Percent dry weight of the combined fractions.
[b] Milligrams as remaining from 1000 mg initial litter.
[c] Less than 0.1%.

A subdivision of these extractives reveals that some components like glucosides, monosaccarides, and myoinositol which are soluble in water were degraded during the first 6 months (Table 3). The large amount found of easily degraded glucose might be explained by a degradation of cellulose by cell-free cellulases and glucosidases which would form glucose as an end product (Berg and Pettersson 1977). A formation of the compounds pinitol and mannitol is also possible.

The light petroleum soluble fraction decreased steadily and only about half the amount remained after 1 year.

TABLE 4. Changes in composition of the solid

	Sample					
	A	B	C	D	E	F
Weight loss of litter (%)	0	10.4	17.8	27.3	43.2	44.4
Lignin						
Relative[a]	30.5	33.5	35.6	39.9	46.2	48.8
Absolute[c]	223	223	233	241	230	243
Neutral carbohydrate constituents[d]						
Relative	46.7	52.7	57.6	52.3	50.0	48.0
Absolute	342	352	377	315	249	232
Calculated as:						
Glucans						
Relative	27.2	31.8	36.9	33.0	25.4	24.0
Absolute	199	212	241	199	126	116
Mannans						
Relative	8.1	8.7	10.3	9.8	9.7	9.1
Absolute	59	58	67	59	48	44
Galactans						
Relative	3.8	4.1	3.9	3.5	3.9	3.6
Absolute	28	27	26	21	19	17
Arabinans						
Relative	5.5	4.1	3.3	2.8	5.7	6.3
Absolute	40	27	22	17	29	30
Xylans						
Relative	2.9	3.3	2.6	2.5	5.0	4.0
Absolute	21	22	17	15	25	19
Rhamnans						
Relative	0.1	0.7	0.6	0.6	0.3	1.0
Absolute	0.7	5	4	4	1	5
Fucosans						
Relative	[e]	[e]	[e]	[e]	[e]	[e]

[a] Given as percent of the dry matter of the solid residue.

[b] Not determined.

[c] Milligrams as remaining from 1000 mg of initial litter.

[d] The acidic carbohydrates (calculated as hexuronides) only determined in samples A–D were 5.2, 6.5, 5.4, and 5.2%, respectively.

[e] Less than 0.1%.

The single components of this fraction showed very differing behaviours, however. Thus, neither the groups of acidic compounds were degraded, nor the pinifolic acid (Appendix). Some alcohols and sterols also appeared to be resistant in this period whereas the hydrocarbons group, steryl esters, sterols, and triglycerides were decomposed rather quickly.

The percentage of ethyl acetate solubles increased during the period as did the absolute amount. As this fraction contains phenolic substances that may inhibit mycelial growth for microfungi from this site (Berg, Hannus *et al.* 1980), it could also be expected to be resistant.

The solid residue

The solid residue disappeared slowly. After 1 year the amount remaining was about 82% and after 5 years about 30% (Table 4, Fig. 2).

During decomposition the different polymer compounds behaved differently both with regard to relative and absolute amounts. Thus, the percentage of single polymer components was often either constant or increased. This increase was most marked for the lignin fraction, which increased from 30.5% of the solid residue up to 57.5 in the last year (Table 4).

We could clearly distinguish that the decrease in absolute amount of the solid components started after different times of incubation, i.e., at differing levels of degradation of the litter. Thus decomposition of the arabinose constituents started first and already during the first summer a weight loss of more than 30% took place (Fig. 3). These are probably present as furanosiresidue during decomposition of litter

G	H	I	J	K	L	M	N	O
51.2	55.8	58.8	63.0	63.8	66.5	70.8	71.4	75.0
50.0 208	49.8 197	nd[b]	54.3 173	52.2 159	54.4 154	57.5 143	54.9 135	56.0 117
37.6 156	39.0 154	nd	37.8 120	40.1 122	38.6 110	36.2 90	38.8 95	44.0 91.9
18.8 78	19.5 77	nd	22.1 70	23.2 71	23.8 68	21.3 53	19.0 47	25.6 53
7.1 29	7.6 30	nd	5.7 18	6.2 19	6.1 17	5.7 14	6.5 16	6.1 14.5
4.0 17	3.4 13	nd	3.4 11	4.0 12	3.1 9	3.6 9	4.4 11	4.4 9
3.3 14	3.8 15	nd	2.3 7	2.3 7	2.0 6	1.7 4	3.2 8	2.2 5
2.9 12	3.5 14	nd	3.6 11	3.4 10	3.4 10	3.1 8	4.6 11	3.9 8
1.5 6	1.2 5	nd	0.7 2	0.9 3	0.2 1	0.8 2	1.1 3	0.8 2
[e]	[e]	nd	[e]	[e]	[e]	[e]	[e]	[e]

dically linked units and are therefore readily hydrolyzable under the acidic conditions in the needles. Initially the decomposition rate was about equal to that of the soluble fractions. The mannans, xylans, and galactans fractions did not show a net loss until after 1 year, whereas the rhamnans fraction remained about constant during the whole period (Fig. 4). For the glucans there was an early net increase before the decomposition started and after 5 years about 75% were decomposed (Fig. 5). For the mannans, galactans, arabinans, and xylans, the corresponding figures were 73, 64, 80, and 48%, respectively. The hemicelluloses as a group were degraded slower than cellulose (Fig. 5), an observation that contrasts with earlier observations. As we thoroughly followed the dynamics of the process this might imply a correction of earlier observations.

Lignin, which is considered to be a slowly decomposed compound, was the last to start degrading and not until 40–45% weight loss of the litter had taken place (after about 1.5–2 years) (Table 2, Fig. 5). The increase in amount taking place during the first 1–2 years probably was due to the formation of humification products. As also the increasing amount of humification products were included in the lignin analysis we have only measured a net loss from this fraction. After 5 years only 48% of the intial amount had decomposed, a low value compared with that for neutral carbohydrate constituents which was about 75% (Table 4).

Conclusions

The low decomposition rate of the phenolic and polyphenolic substances is probably due to their inhibit-

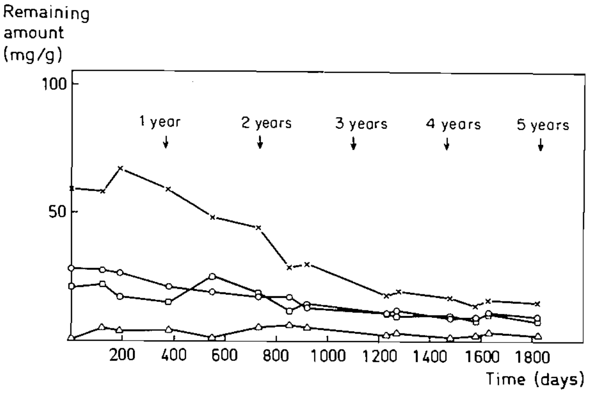

FIG. 4. The degradation of four of the hemicelluloses given as remaining amount from initially 1 g of litter. ×, mannans; ○, galactans; □, xylans; △, rhamnans.

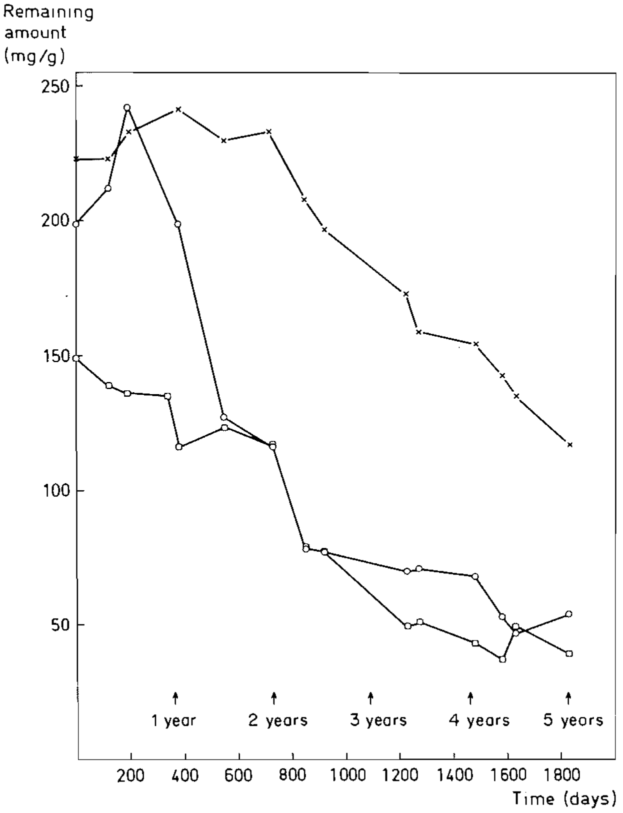

FIG. 5. The degradation of lignin (×), cellulose (○), and the combined hemicelluloses group (□). Remaining amount from initially 1 g of litter.

ing properties on fungal growth (Berg, Hannus *et al.* 1980), and they could be the reason for the slow increase of fungal mycelium in the litter (Berg and Söderström 1979).

The percentage of lignin increased all the time and the proportions between lignin and the combined fraction of cellulose and hemicellulose remained about constant from 1.5 to 2 years and onwards. It thus appears reasonable to conclude that the decomposition rate of the lignin fraction becomes rate determining for the decomposition of the whole litter after 2 years (about 45% weight loss). Such a rate regulating function has been suggested earlier by Van Cleve (1974) and Fogel and Cromack (1977).

It is noteable that the level of lignin and humification products is so much greater in the highly decomposed needles than in the underlying humus in the forest system (A_{01}–A_{02} layer) studied (Staaf and Berg 1977). On the other hand, possibly only a very tiny part of the needle litter will reach this layer. Needle fragments in an advanced state of decomposition were found in the dead moss part of the A_{00} layer, a position that also the litter bags had reached after 5 years. With a similar degradation rate for the remaining 25% of litter, we might expect that a very small part of this major litter component will contribute to the humus layer. The A_{01}–A_{02} layer thus might be composed of root litter remnants, especially as there is a high formation of root litter at this site (Persson 1980).

Acknowledgements

The skilful technical assistance of Mrs. Gunnel Fransson and Mr. Seved Helmersson and the financial support from Carl Tryggers Foundation is gratefully acknowledged. Mr. Bengt Söderström who supplied us with the fungal strains and Professor E. Haslam who helped us with a sample of procyanidine (B 3) are gratefully acknowledged. Part of the work was carried out within the Swedish Coniferous Forest Project.

ANONYMOUS. 1974. Continuation proposal 1974/1975. Description of the project. Memo report. Swedish Coniferous Forest Project. Swedish Univeristy of Agricultural Sciences, Uppsala.

AXELSSON, B., and S. BRÅKENHIELM. 1980. Investigation sites of the Swedish Coniferous Forest Project — biological and physiological features. *In* Structure and function of northern coniferous forests. An ecosystem study. Ecol. Bull. **32**: 25–64.

BERG, B., K. HANNUS, T. POPOFF, and O. THEANDER. 1980. Chemical components of Scots pine needles and needle litter and inhibition of fungal species by extractives. *In* Structure and function of northern coniferous forests. An ecosystem study. Ecol. Bull. **32**: 391–400.

BERG, B., U. LOHM, H. LUNDKVIST, and A. WIRÉN. 1980. Influence of soil animals on decomposition of Scots pine needle litter. *In* Structure and function of northern coniferous forests. An ecosystem study. Ecol. Bull. **32**: 402–409.

BERG, B., and G. PETTERSSON. 1977. Location and formation of cellulases in *Trichoderma viride*. J. Appl. Bacteriol. **42**: 65–75.

BERG, B., and B. SÖDERSTRÖM. 1979. Fungal biomass and nitrogen in decomposing Scots pine needle litter. Soil Biol. Biochem. **11**: 339–341.

BERG, B., and H. STAAF. 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. *In* Structure and function of northern coniferous forests. An ecosystem study. Ecol. Bull. **32**: 373–390.

——— 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. *In* Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts. Ecol. Bull. **33**: 163–178.

Bethge, P. O., R. Rådeström, and O. Theander. 1971. Kvantitativ kolhydratbestämning — en detaljstudie. Communication from Swedish Forest Product Research Lab. 63 B. S-114 86 Stockholm. (In Swedish.)

Bylund, M., and A. Donetzhuber. 1968. Semi-micro determination of uronic acids. Sven. Papperstidn. **15**: 505–508.

Fogel, R., and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in Western Oregon. Can. J. Bot. **55**: 1632–1640.

Gosz, I. R. 1981. Nitrogen cycling in coniferous ecosystems. *In* Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts. Ecol. Bull. **33**: 405–426.

Handley, W. R. C. 1954. Mull and mor formation in relation to forest soils. Forestry Commission Bulletin No. 23. pp. 1–115.

Hannus, K., and G. Pensar. 1974. Silvichemicals in technical foliage. II. Nonpolar lipids in the technical foliage of Scots pine. Finn. Chem. Lett. **1**: 255–262.

Harrison, A. F. 1971. The inhibitory effect of oak leaf litter tannins on the growth of fungi, in relation to litter decomposition. Soil Biol. Biochem. **3**: 167–172.

Hayes, A. J. 1965. Studies on the decomposition of coniferous leaf litter. I. Physical and chemical changes. J. Soil Sci. **16**: 121–140.

Louisier, J. D., and D. Parkinson. 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. **54**: 419–436.

Melin, E. 1928. Biological decomposition of some types of litter from North American forests. Ecology, **11**: 72–101.

Persson, H. 1980. Spatial distribution of fine-root growth, mortality and decomposition in a young Scots pine stand in Central Sweden. Oikos, **34**: 77–87.

Popoff, T., and O. Theander. 1977. The constituents of conifer needles. VI. Phenolic glycosides from *Pinus silvestris* L. Acta Chem. Scand., Ser. B, **31**(4): 329–337.

Staaf, H., and B. Berg. 1977. A structural and chemical description of litter and humus in a mature Scots pine stand at Ivantjärnsheden. Swedish Coniferous Forest Project. Internal Report No. 65.

——— 1981. Plant litter input to soil. *In* Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts. Ecol. Bull. **33**: 147–162.

Swanger, G. 1974. Component decomposition rates in coniferous forest litter. Doctoral dissertation. University of Idaho, Moscow, Idaho.

Tenney, F., and S. A. Waksman. 1929. Composition of natural organic materials and their decomposition in the soil. IV. The nature and rapidity of decomposition of the various organic complexes in different plant materials, under aerobic conditions. Soil Sci. **28**: 55–84.

Theander, O. 1978. Leaf litter of some forest trees. Chemical composition and microbial activity. Tappi **61**(4): 69–72.

Theander, O., and P. Åman. 1976. Low-molecular carbohydrates in rapeseed and turnip rapeseed meals. Swed. J. Agric. Res. **6**: 81–85.

Van Cleve, K. 1974. Organic matter quality in relation to decomposition. *In* Soil organisms and decomposition in tundra. Tundra Biome Steering Committee, Stockholm. pp. 311–324.

Appendix

Changes in composition of the main constituents in the light petroleum fractions during decomposition[a]

	Sample			
	A	B	C	D
Weight loss of the litter	0	10.4	17.8	27.3
Hydrocarbons	2.7	2.4	1.6	1.1
Sesquiterpenes	2.7	2.4	1.6	1.1
δ-Cadinene	0.9	0.7	0.4	0.2
γ-Cadinene	0.7	0.6	0.5	0.4
β-Carophyllene	0.2	0.1	0.1	[b]
Diterpenes	[b]	[b]	[b]	[b]
Steryl esters	6.5	8.0	5.6	4.2
Acids				
16:0	0.3	0.4	0.2	[b]
9-18:1	0.2	0.2	0.1	[b]
9,12-18:2	0.4	0.4	0.1	[b]
5,9,12-18:3	0.2	0.2	0.1	[b]
9,12,15-18:3	0.1	0.1	[b]	[b]
5,11,14-20:3	0.2	0.2	0.1	[b]
Sterols				
β-Sitosterol	2.7	3.2	2.3	1.5
β-Sitostanol	0.4	0.6	0.4	0.5
Cycloartenol	0.3	0.4	0.3	0.2
Triglycerides	8.1	2.8	2.9	3.2
Acids				
16:0	0.8	0.2	0.2	0.2
9,18:1	0.8	0.3	0.4	0.3
9,12–18:2	0.8	0.3	0.4	0.4
5,9,12–18:3	0.1	[b]	[b]	[b]
9,12,15–18:3	1.1	0.2	0.3	0.1
5,11,14–20:3	[b]	[b]	[b]	[b]
Acidic compounds	14.3	15.3	20.9	21.6
Fatty acids	1.6	2.6	2.1	2.3
16:0	0.4	0.4	0.5	0.4
9,18:1	0.2	0.2	0.4	0.3
9,12–18:2	0.2	0.2	0.4	0.5
5,9,12–18:3	0.1	0.2	0.5	0.4
9,12,15–18:3	0.1	[b]	[b]	[b]
Diterpene acids	12.7	12.7	18.8	19.3
Abietinic	0.4	0.2	0.2	0.2
Dehydroabietinic	2.7	2.5	3.0	3.2
Pinifolic	7.3	9.3	12.1	12.3
Alcohols and sterols	6.6	8.1	6.9	9.3
Isoabienol	3.6	2.0	1.3	1.3
n-Nonacosan-10-ol	1.5	2.4	2.5	4.7
β-Sitosterol	1.3	3.4	2.7	3.0

[a] Given as percent of the dry matter of the fractions.
[b] Less than 0.1%.